Two Studies on the Interplay between Social Preferences and Individual Biological Features

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Two Studies on the Interplay between Social Preferences and Individual Biological Features

Running headline: Biological features and social preferences

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ABSTRACT

Biological features and social preferences have been studied separately as factors influencing human strategic behaviour. We run two studies in order to explore the interplay between these two sets of factors. In the first study, we investigate to what extent social preferences may have some biological underpinnings. We use simple one-shot distribution experiments to attribute subjects one out of four types of social preferences: Self-interested (SI), Competitive (C), Inequality averse (IA) and Efficiency-seeking (ES). We then investigate whether these four groups display differences in their levels of facial Fluctuating Asymmetry (FA) and in proxies for exposure to testosterone during phoetal development and puberty. We observe that development-related biological features and social preferences are relatively independent. In the second study, we compare the relative weight of these two set of factors by studying how they affect subjects' behaviour in the Ultimatum Game (UG). We find differences in offers made and rejection rates across the four social preference groups. The effect of social preferences is stronger than the effect of biological features even though the latter is significant. We also report a novel link between facial masculinity (a proxy for exposure to testosterone during puberty) and rejection rates in the UG. Our results suggest that biological features influence behaviour both directly and through their relation with the type of social preferences that individuals hold.

Keywords: Testosterone; Ultimatum Game; Fluctuating Asymmetry; Facial masculinity; 2D:4D; Social preferences.

1. Introduction

In the last few years, experimental methods have been used to explore how biological features relate to individual behaviour in strategic situations. These laboratory experiments have employed a number of simple games long-studied in Experimental Economics (Smith, 1987). These games embody simplified social interactions in which the payoffs that subjects obtain depend both on their own decisions and the decisions of others. These experiments generate results which are easily measurable, quantifiable and replicable. The biological features studied in this literature include the impact of hormones and their receptors (Kosfeld et al., 2005; Burnham, 2007; Zak et al., 2007; Crockett et al., 2008; Knafo et al., 2008; Zak et al., 2009; Eisenegger et al., 2010), genetic differences (Wallace et al., 2007; Cesarini et al., 2008), neural factors (Fehr & Rangel, 2011), and the effect of developmental instability, proxied by Fluctuating Asymmetry (Zaatari & Trivers, 2007; Zaatari et al., 2009; Sanchez-Pages & Turiegano, 2010).

These studies have also shed new light on the wide array of results in economic experiments showing that many individuals care strongly about the whole distribution of income and not only about their own material payoff. This class of concerns receive the name of *social preferences* in Economics. Social preferences have been extensively studied and include inequality aversion (Fehr & Schmidt, 1999; Bolton & Ockenfels, 2000; Binmore & Shaked, 2010), joint welfare maximization (Charness & Rabin, 2002), and competitive preferences (Frank, 1987; Charness & Grosskopf, 2001). Social preferences have been studied extensively in Psychology under the rubric of Social Value Orientation (for reviews see Balliet, et al., 2009 and Murphy & Ackerman, 2012)

Research in Experimental Economics typically uses observed choices to uncover unobservable individual heterogeneity in social preferences. This is called the *revealed preference* approach. On the other hand, research in Biology uses individual heterogeneity (in physiological features, for instance) to explain observed differences in behaviour. The present paper aims at building a bridge between these two approaches. To this end, we run two studies. The first one explores the extent to which individual biological features and social preferences are independent of each other. The second study explores, within the same population, the relative importance of these two sets of variables in strategic interactions by relating them to behaviour in the Ultimatum Game (UG henceforth).

Study 1

In the first step of this study, we use a set of one-shot distribution experiments to classify subjects into one of the main four types of social preferences described in the Experimental Economics literature (Engelmann & Strobel, 2004): Self-interested (SI), Competitive (C), Inequality averse (IA) and Efficiency-seeking (ES). These four types of social preferences translate into different behaviours in economic interactions. SI subjects are mainly interested in maximizing their own payoff. The ES subjects are interested in maximizing the total benefits obtained by all participants, even at their own expense. IA subjects are interested in minimizing the disparity in the distribution of income independently of whether this disparity is in their favour or not. Finally, C subjects are interested in minimizing unfavourable inequality and in maximizing favourable inequality, even at the expense of some material payoff.

Once classified, we study whether subjects who hold different social preferences display differences in several biological features. The biological features which we consider here are facial Fluctuating Asymmetry (FA, henceforth), and two proxies for testosterone exposure in utero and during puberty, the second to fourth digit ratio (2D:4D) and facial masculinity, respectively. We have chosen these variables because they have showed to influence a number of behaviours (e.g. tendency to cooperate, competitiveness), which are affected by social preferences as well. Their impact on adult behaviour operates through their effect on nervous system development (Bates, 2007; Berenbaum & Beltz 2011).

FA refers to minor non-directional deviations from bilateral symmetry (Palmer & Strobeck, 1986). It is considered to be the result of developmental instability. Many studies show a link between symmetry and individual fitness, both in non-humans (Møller, 1997; Møller, 2006), and in humans (Van Dongen & Gangestad, 2011). Facial symmetry has been proposed as a cue of heritable fitness benefits (Scheib et al., 1999; Little & Jones, 2006). Regarding human behaviour, low FA is linked to individuals who are more self-confident, prone to behave aggressively (Furlow et al., 1998; Manning & Wood, 1998; Benderlioglu et al., 2004) and less cooperatively (Sanchez-Pages & Turiegano, 2010).

Testosterone (T) is a steroid hormone which promotes behaviours aimed at increasing reproductive success in males, such as risk-taking (Mazur & Booth, 1998) aggression (Archer, 2006), sensation-seeking (Roberti, 2004) and interest in sex (Rupp & Wallen, 2007). T levels have been described to correlate with general fitness, reproductive success and status (Mazur & Booth, 1998; Bribiescas, 2001; Zitzmann & Nieschlag, 2001; Muehlenbein & Bribiescas, 2005). In addition, T exerts organizational effects on the brain during phoetal sexual differentiation (Morris et al., 2004), and during puberty (Sisk et al., 2003). Exposure to T in these critical periods is considered to have an effect on brain structures and, therefore, on adult male behaviour (Berenbaum & Beltz 2011). We use 2D:4D and facial masculinity as proxies for the level of exposure to the hormone in these two developmental stages. Evidence indicates that 2D:4D negatively correlates with prenatal testosterone (Lutchmaya et al., 2004; Zheng & Cohn, 2011). Low 2D:4D subjects are also less likely to behave altruistically (Millet & Dewitte, 2006; Sanchez-Pages & Turiegano, 2010). But, as 2D:4D is related to dispositional dominance, low ratios associate as well with pro-social behaviour in certain contexts (Millet, 2011). On the other hand, many masculine facial features develop during puberty under the action of testosterone (Enlow, 1996). Facial masculinity has been shown to affect human male behaviour (Apicella et al., 2008; Pound et al., 2009). Finally, given that some authors have linked facial masculinity to male attractiveness (Johnston, 2006; Rhodes, 2006), we conjecture that facially masculine men might behave similarly to attractive men (Takahashi et al., 2006; Wilson & Eckel, 2006).

To the best of our knowledge, no previous study has investigated the link between the social preferences considered in Economics and the biological features considered in the present work (but see Yamagishi et al., 2012). Hence, our conjectures on the existence of differences in biological features across social preference groups or on the direction of these differences (if any) cannot be strongly substantiated by previous results. Still, related evidence suggests that subjects less interested in their relative position in the income distribution (SI and ES) should show lower levels of facial masculinity given the relation described between testosterone and status-seeking behaviour (Mazur & Booth, 1998;

Josephs et al., 2006). We predict a similar pattern for 2D:4D (Millet & Dewitte, 2006) although we expect IA subjects, who are the most interested in implementing an egalitarian distribution of income, to show the lowest levels (Van den Bergh & Dewitte, 2006; Millet & Dewitte, 2009). Regarding FA, individuals less interested in joint welfare (SI and C) are expected to display lower levels of FA since more symmetric individuals are less interested in cooperation given that they need less support from their peers (Zaatari & Trivers, 2007; Sanchez- Pages & Turiegano, 2010). This difference in FA is expected to be greatest between SI an ES subjects, as SI subjects do not care about the outcome received by others whereas ES subjects care mostly about joint welfare.

Study 2

In the second study, we compare the relative importance of individual biological features and social preferences in strategic interactions by looking at subjects' behaviour in the UG. In this experiment, two players have to divide a sum of money. The first player proposes how to divide the sum between the two players. The second player can either accept or reject this proposal. A rejection implies that both players receive nothing. Acceptance implies that the money is split according to the proposal. This game is well suited for our purposes because of two reasons. First, it is well-known that behaviour in the UG departs substantially from the standard economic prediction of own income maximization. Pure self-interest dictates that responders should accept any positive offer and that proposers should make the lowest possible offer. However, low offers are often rejected and the vast majority of offers range between 30% and 50% of the sum to be distributed (Roth, 1995). The second reason is that the UG has been widely employed in the study of the effects of hormones on behaviour (Kosfeld et al., 2005; Burnham, 2007; Zak et al., 2007; Crockett et al., 2008; Zak et al., 2009; Zethraeus et al., 2009; Eisenegger et al., 2010), and of development-related variables, like FA (Zaatari & Trivers, 2007; Zaatari et al., 2009) and 2D:4D (Van den Bergh & Dewitte, 2006).

In the role of responders, we expect SI and ES subjects to accept lower offers than the rest of participants; the SI group because they prefer any positive amount of money to nothing, and the latter because rejection entails the loss of the whole amount to be distributed. On the other hand, C subjects should reject low offers more often because acceptance would leave them significantly worse off than the proposer. IA subjects should reject low offers too in order to avoid a high disparity in the earnings of the two participants. In the role of proposers, we expect IA and ES subjects to make higher offers than the rest, given that IA agents care strongly about equality and that ES subjects can reduce the risk of rejection (that would lead to the whole sum being wasted) by doing so. This leads us to expect that the offers made by SI and C subjects should be lower in average than those made by IA and ES.

In addition to the relationships already described in the literature between biological features and behaviour in the UG, (Van der Bergh & Dewitte, 2006; Zaatari & Trivers, 2007), we also expect participants who reject low offers to show higher facial masculinity. We base this prediction on 1) the link between masculine features and self-sufficiency (Muehlenbein & Bribiescas, 2005), and 2) the higher rejection rates of unfair splits displayed by males with higher testosterone levels (Burnham, 2007), and 3) the known effect of facial attractiveness, which partially relates to masculinity, on reciprocity (Wilson & Eckel, 2006). Finally, in the role of proposers, we expect participants exposed to low levels of testosterone during development (with higher 2D:4D or lower facial masculinity) to make higher offers. This hypothesis is based on the interpretation of fairness in the UG as an expression of cooperation (Page et al., 2000) and on the relationship between cooperation and exposure to testosterone during development (Millet & Dewitte, 2006; Sanchez-Pages & Turiegano, 2010).

2. Methods

Preliminaries

The two studies we report here were performed successively in Madrid in the winter of 2009. A total of 152 self-declared white male subjects participated, distributed in 10 morning sessions with less than 20 subjects each. Participants were recruited by e-mail. All of them filled a short questionnaire asking their age, discipline of study, ethnicity and sexual orientation. Subjects were students at the Universidad Autónoma de Madrid (UAM), mostly from the School of Biological Sciences. Ages varied from 17 to 30, 20.34±0.17yr; av±SEM). Participants gave their written consent to the use of their data. The experiment was approved by the Ethics Committee of the UAM.

Subjects were seated at partitioned computer terminals to ensure they could not interact with each other. All subjects were carefully instructed about the rules of the experiment. The experiment was conducted via computers employing the z-Tree 3.2.10 software for Economics Experiments (Fischbacher, 2007). Subjects were informed that their payment could reach around 9€ and it was going to depend on some of the choices they were about to make, although they did not know which ones specifically. Hence, all decisions mattered for participants. Actual payments were computed based on all their decisions except for their choice as proposers in the UG. We informed subjects of this payment method a few weeks after the experimental sessions finished in order to avoid information spreading. Payoffs during the experiment were expressed in points, and participants knew that the exchange rate was 100p=2€. At the end of each session, subjects were paid privately in cash. The average amount paid was 8.43±0.43€ (av±SD), including a show-up fee (5€). The experimental sessions took about 30 minutes. No female was present during the sessions nor the process of data collection in order to avoid any moderating effects of sexual cues on participants' behaviour (Van der Bergh & Dewitte, 2006).

Measurement of individual biological features

Photographs of the participants and scans of their hands were taken before each session. We took high-resolution full frontal facial colour photographs of all participants with an Olympus E-500 digital camera. The photos were taken in homogeneous conditions (soft light, fixed distance of the camera, completely opened zoom to avoid any optical distortion). Participants were asked to remove any facial adornment and to pose with a neutral expression. We tried to minimize any distortion caused by the rotation of the head by asking subjects to look directly into the camera, and by correcting their position if necessary (instead of using a more osteological standardization, such as the Frankfort Horizontal). We took three images of each participant.

The shape of each face was defined by manually setting 39 landmarks (LM) which can be unambiguously identified in every photo (Sanchez-Pages & Turiegano, 2010) by using the TPS morphometric free software (by F.J. Rohlf, see http://life.bio.sunysb.edu/morph/). We employed these LMs to calculate facial masculinity and FA using the Morpho-J free software (by C. P. Klingenberg. See http://www.flywings.org.uk/MorphoJ_page.htm). The LMs were placed twice, once for each researcher, allowing the software to quantify digitizing error through Procrustes ANOVA analysis (Klingenberg & McIntyre 1998; Klingenberg et al. 2002).

Individual FA was calculated employing a Procrustes ANOVA analysis (Klingenberg & McIntyre 1998; Klingenberg et al. 2002). We placed LMs in two photos of each subject in order to control for any error in the photo taking process. We thus quantified two measurement errors, in photo taking and the digitizing error. There was a significant directional asymmetry in the sample, that is, the mean asymmetry was significantly different from zero (the main effect of mirroring is significant in the Procrustes ANOVA; $F=4.34$ $df=37$ $p<0.001$). Individual FA scores correspond to the Procrustes distance between the original and mirrored copies of the landmark configuration of each individual after correcting for directional asymmetry (Klingenberg & McIntyre, 1998; Schaefer et al., 2006).

Facial masculinity was measured by calculating the Procrustes distance between the LM configuration of each male average image and a reference female face (Sanchez-Pages & Turiegano, 2010). The reference female face was obtained by averaging 50 images of white self-reported female students and their mirror images. Each male average face was obtained from two photos of each participant and their mirror images. We employed this protocol in order to avoid any perturbation in this measurement caused by the asymmetry of males faces compared to the female reference face. An advantage of this method is its independence from age and ethnic differences (given the appropriate reference group).

Participants' right hands were scanned with a CanoScan LiDE70 high-resolution scanner. The second and fourth digits were measured from the centre of the flexion crease proximal to the palm to the top of the digit. This is a commonly accepted method to calculate 2D:4D (Fink et al., 2005; Millet & Dewitte, 2006; Apicella et al., 2008). The fingers were measured twice (once by each author) employing the appropriate utility of the TPS morphometric free software. Both measures highly correlated ($r = 0.985$, $p < 0.001$ and $N = 152$). The variable employed in the analyses was the average of both measures.

Study 1

In the first study, we measured social preferences with a sequence of two-choice questions presented to subjects, our Social Preferences Test (SPT). Answering to a sequence of questions is a method commonly employed when measuring social preferences (Van Lange et al., 1997).The choices in the SPT were two distributions of points between the subject and a counterpart. Subjects were told that this counterpart was a participant in future experimental sessions. In the first pair of choices, subjects had to choose between distribution A= {20, 30} and distribution B= {30, 80}, where the first figure indicates the number of points allocated to the subject making the choice. These distributions displayed inequality unfavourable to the subject. In the second pair of distributions, the inequality was favourable to the subject, who was asked to choose between distribution C= {70, 10} and D= {60, 50}. These two pairs of distributions are such that the four possible different profiles of choices correspond to four different types of social preferences. The choice {B, C} corresponds to SI subjects, that is, those mostly interested in maximizing the amount of points they receive. The choice {B, D} corresponds to ES subjects, that is, those interested in maximizing the total sum of points. The choice {A, D} corresponds to IA subjects because those choices yield the most egalitarian distribution of points within each pair. Finally, we attribute the remaining choice to C subjects, that is, those interested in minimizing unfavourable inequality and in maximizing favourable inequality, even at the expense of some material payoff.

Our SPT was designed along the same lines as the well-established Triple-Dominance Measure of Social Value Orientation (SVO) (Van Lange et al., 1997). This measure presents subjects with nine questions, each containing three distributions of income. Each of these three items corresponds to a primary SVO: prosocial, individualistic and competitive. A subject who picks six or more items corresponding to one of these SVOs is classified as such. Hence, the Triple-Dominance measure of SVO may leave unclassified a non-negligible fraction of subjects (Eek & Gärling, 2006). We designed our SPT in order to classify all participants. This *efficiency* property (Murphy et al., 2011) is important, especially when subjects are paid for their choices. More importantly, the SPT permits a finer classification of subjects: the Triple-Dominance Measure of SVO contains no item in which the subject experiences unfavourable inequality, and therefore it cannot distinguish between IA and ES subjects, classifying both of them as prosocial. In addition, the SPT is simple and provides clear economic incentives. Still, given that the SPT is based on a small number of questions, we checked its validity by comparing it to the Triple-Dominance Measure of SVO.

We ran this robustness study at UAM in the fall of 2011 and 2012. A total of 106 self-declared white males subjects (age 20.85±0.19yr) were presented with the nine items of the Triple-Dominance Measure of SVO and the two choices of our SPT. Subjects were informed that they would be paid for the eleven options they chose. Results of this study showed a high degree of consistency between the Triple-Dominance Measure of SVO and the SPT. The SPT produced a classification which coincided with the SVO measure for 90.4% of the subjects that the SVO test classified (12 out of the 106 subjects were left unclassified by the SVO). Let us reiterate that subjects classified as either IA or ES in the SPT are classified as prosocial in the Triple-Dominance Measure of SVO. In February 2013, we checked the reliability of our SPT by asking these participants to answer again the SPT through e-mail (but without a payment). We recruited 79 of the initial 106 participants. Of these participants, 84.8% (n=67) did not change of SPT group. The more stable group was SI (94.4% of the initial SI maintained this classification). The most frequent change in group was between IA and EM (3 of the 13 initial IA became classified as EM).

Study 2

In the second study, participants took part in four one-shot UGs. Participants were asked to make choices in both roles, as responders and as proposers. In order to avoid competitive effects within each group of participants, subjects were playing each time against a participant not present in the room. As proposers, subjects could offer any integer amount of points between 0 and 100p to a future participant. As responders, they played three times; they were told that they were playing against three previous participants. Each time they had to accept or reject a different offer: a low offer (15p), an intermediate offer (30p) and a high offer (50p). The order of these three offers was randomly chosen in each session. Given that subjects had to make an offer to a future participant as proposers, it was natural for them to receive offers from previous participants in the role of responders. We chose this design over asking subjects for their minimal acceptable offer because that design makes less clear for subjects how choices determine payments. The high offer (50p) served as a control to ensure that subjects understood the experiment. All subjects accepted that offer, so we will not include it in any further analysis.

Statistical analyses

Table 1 provides summary statistics of the morphological variables we employ. We tested the normality of these variables with the Kolmogorov-Smirnov test. Masculinity and 2D:4D are normally distributed. We log transformed FA after multiplying the measure by 100 (in order to avoid negative values which could complicate the interpretation of its effects). Offer was resistant to any transformation into normality, so when performing any analysis with this variable we used non-parametric methods. To analyze the results we employed ANOVA and student-t test for differences in normally distributed variables, Kruskal-Wallis H for non-normally distributed variables (i.e., Offer) and chi square test when comparing nominal variables. When analyzing correlation between variables, we used the non-parametric Spearman ρ. We also employed logistic regressions to analyze simultaneously the effect of several independent variables on our dichotomous dependent variables (acceptance or rejection of the low and medium offers). These analyses were made following the recommendations in Kleinbaum & Klein (2002). First, the effects of individual variables were analyzed independently. New variables were subsequently added to these models. We do not report results on interactions between variables because they were not significant. We employed SPSS15 in all our statistical analysis.

3. Results

Study 1

In the first study, we classified the 152 subjects according to their answers in the SPT. The most common social preference group among our participants was SI (51.32%, n=78), followed by C (23.03%, n=35), ES (20.39%, n=31), and finally IA (5.26%, n=8). There were statistically significant differences (Chi square test, χ^2_3=9.208, p=0.027) between subjects who were studying Economics (n=55) and those who were studying Biology (n=81); the former type of students displayed a higher proportion of SI subjects (SI=61.8%; ES=21.8%; C=16.4%; IA=0%) whereas the latter displayed a higher proportion of C subjects (SI=44.4%; ES=18.5%; C=27.2%; IA=9.9%).

Next we analyzed how biological features varied across these groups (Figure 1). We found no significant differences in 2D:4D (ANOVA, $F_{148, 3}$=0.746, p=0.527) nor in facial masculinity ($F_{148, 3}$=0.579, p=0.630). We also found that, as we initially conjectured, SI subjects show lower levels of FA than ES subjects (t test, t_{107}=2.043, p=0.043). Differences are not significant across all four groups ($F_{148, 3}$=2.056, p=0.109), although they follow the predicted pattern (see Figure 1).

Study 2

In the role of proposers, the average offer made across all subjects was 44.84 points. We found significant differences in the average offer across groups (Kruskal-Wallis test, H_3=9.598, p=0.022). Figure 1.C shows that SI and C subjects make lower offers on average than the ES and IA subjects as predicted. Neither 2D:4D (Spearman correlation coefficient,

ρ_{152}=0.031, p=0.702), facial masculinity (ρ_{152}=-0.032, p=0.692) nor FA (ρ_{152}=-0.065, p=0.430) show a significant correlation with the offer for the entire subject pool.

Regarding their behaviour as responders, 31.57% of subjects rejected the medium offer whereas 58.55% rejected the low offer. There were significant differences in rejection rates across the SPT groups, both for the medium (Chi square test, χ^2_3=11.261, p=0.010) and the low offer (χ^2_3=9.944, p=0.019). Figure 1 shows that, as expected, SI and ES agents accept both offers more often, whereas C subjects reject them more frequently.

As the first step in the simultaneous analysis of the importance of biological features and social preferences, we analyzed the effect of the former set of factors on responders' behaviour (see Table 2 for p-values and statistics). Participants who rejected the low offer had higher facial masculinity than those who accepted it. We found no differences in FA between subjects who accepted or rejected the low offer, in line with previous results in the literature (Zaatari & Trivers, 2007). We found no significant differences in 2D:4D either, although average digit ratios followed the pattern (lower ratios in participants who rejected the offer) previously reported in the literature (Van den Bergh & Dewitte, 2006). We performed the same analysis for the medium offer and we found identical patterns for the three variables, although none of the differences were statistically significant ("medium offer" row in Table 2).

Finally, we evaluated simultaneously the effect of all variables on acceptance rates by running a logit regression analysis (Table 3). The analysis of the low offer showed a significant effect of the SPT classification in the same direction as in the results described above. Facial masculinity had a negative impact on the acceptance rate of the low offer. The logit analysis of the medium offer yielded that the SPT classification had a significant impact on acceptance rates, whereas no biological variable was found to have a significant effect (lower half of Table 3).

4. Discussion

Inequality aversion and efficiency concerns on the one hand (Fehr & Schmidt, 1999; Charness & Rabin, 2002; Engelmann & Strobel, 2004), and exposure to hormones and proxies for developmental instability on the other (Kosfeld, et al., 2005; Van den Bergh & Dewitte, 2006; Burnham, 2007; Zaatari & Trivers, 2007; Zak et al., 2007; Apicella et al., 2008; Crockett et al., 2008; ; Zak et al., 2009; Eisenegger et al., 2010), can explain why the behaviour observed in economic experiments departs from the predictions of standard economic theory. In this paper, we offer a systematic attempt at linking social preferences, individual biological features and strategic behaviour.

In a first study, we found that these two sets of explanations are related only to some extent. Two different social preference groups, SI and ES, which account for 71.71% of the subject pool, displayed differences in FA, a biological feature that has been shown to affect behaviour in economic games. No significant differences were found in facial masculinity or 2D:4D across social preference groups. The link between social preferences and individual biological differences would thus seem of relatively low importance, at least under our measure of social preferences. We measured social preferences by means of the

SPT, a set of one-shot distribution experiments whose results are highly consistent with the widely-used Triple- Dominance Measure of SVO (Van Lange et al., 1997). This measure is also highly reliable. The STP is more efficient than the Triple- Dominance Measure of SVO since it classifies all subjects, and it is also finer since it can single out inequality averse subjects. Both the SPT and SVO are designed to shut down strategic concerns such as reciprocity that could potentially confound with purely distributional concerns. However, none of these two measures can rule out that subjects may have reputation-management concerns when making one-shot distributional choices (Trivers, 2004). Another weakness of both measures is their limited statistical power resulting from their use of a categorical classification instead of a continuous one. We cannot rule out that the SPT does not have the statistical power required to detect subtle but yet important biological effects. In our future research, we plan to investigate further this issue by using the Slider Measure developed by Murphy et al. (2011) given its higher statistical power.

In the second study, we looked at the effect of social preferences (measured by the SPT) and individual biological features in behaviour in the UG. The four SPT groups behaved differently in both roles, as we had predicted (see Figure 1B, C). As a matter of fact, social preferences measured with the SPT seem to have a stronger effect on behaviour than the biological features studied here. When we include both the SPT classification and the set of physiologically-based variables in the analysis of acceptance rates (see Table 3), the former is always significant, whereas the latter is significant only for the low offer. This suggests that the importance of biological features might be crowded out by financial incentives. In the role of proposers, there are differences in the amount offered by the four groups, but there is no correlation between the offer made and any biological feature we considered. These results suggest that social considerations have an effect at least as strong as biological features (Eisenegger et al., 2010; Salvador, 2005). This conclusion, however, can apply to neutral contexts only. Previous studies have shown that modest situational cues can alter the relationship between biological features and the behaviour of males in the UG (Van den Bergh & Dewitte, 2006). This is consistent with results showing that behaviour in the UG rests on a balance between phylogenetically older structures, involved in automatic reactive emotional responses (amygdala), and the neocortical areas, which have a richer future representation (frontal cortex and insula) (Gospic et al., 2011). While biological characteristics are important in the emotional response to a challenge, they are less important in the evaluation of long-term consequences. The presence of situational cues inducing stronger emotional responses (Van den Bergh & Dewitte, 2006; Millet & Dewitte, 2009) might enhance the influence of biological features on strategic behaviour.

But the effect of social preferences and biological features cannot be completely decoupled. Biological features have an effect on behaviour through social preferences. We obtained that SI and ES subjects have different levels of FA and also make different offers in the UG. This suggests that the positive link between FA and offers in the UG observed in Zaatari & Trivers (2007) could be attributed to two specific subsets of the population, one interested in maximizing efficiency and another purely self-interested. Probably, this correlation between FA and the offer in the UG for just a part of the subject pool rather than for the entire sample constitutes our major departure from the previous literature. However, there are three important differences between Zaatari & Trivers (2007) and our work that make comparisons difficult. First, the vast majority of their subjects were teenagers (mean age= 15.93 years; S.D.=1.67; mode=15; range=13–20) while ours were young adults (our subjects ages varied from 17 to 30, with a mean of 20.34±0.17 years and a mode of 20). This is an important difference that is even more relevant at the light of 1) the described effects of T on behaviour in the UG (Burnham, 2007) and 2) that teenagers suffer rapid changes in T levels (Buchanan et al., 1992; Sisk & Zehr, 2005). Another main difference is that these authors measured asymmetry in several body characteristics, and attributed them entirely to FA. In our analysis, we measured FA separating it from any possible directional asymmetry (Schaefer et al., 2006). Third, these authors obtained the result linking low FA to low offers after a statistical correction of the so-called background variables (age, sex, body mass index and friendliness scores). We did not control for these measures (except for age) and this adds another source of non-comparability.

The present paper also shows the influence of facial masculinity on behaviour. Facial masculinity is a proxy for exposure to testosterone during puberty (Enlow, 1996). This variable is an objective measure, in contrast with often-used measures of masculinity based on subjective scores. Objective measures of facial masculinity have been rarely used in behavioural research (Apicella et al., 2008; Carré & McCormick, 2008; Pound et al., 2009) and, with the exception of Sanchez-Pages & Turiegano (2010), they have not been used to study strategic behaviour. The immuncompetence handicap hypothesis states that masculine traits signal inmunnocompetence and developmental stability (Folstad & Karter, 1992). In this line, perceived facial masculinity correlates both with health (Rhodes et al., 2003) and strength (Fink et al., 2007) in young males. Therefore, men with more masculine faces seem to be more capable of resisting physiological stress and, to some extent, could be said to show higher phenotypic quality.

Our results for the UG seem plausible if one considers the game, as some authors do (Page et al., 2000), as an approximation to the problem of dividing the expected catch in hunting, where rejection means a refusal to cooperate. Given that males seem to adopt different behavioural strategies depending on their phenotypic quality (Zaatari & Trivers, 2007; Apicella et al., 2008), more masculine males might not need to be as cooperative as less masculine males because their greater ability to gain access to resources. This hypothesis has also been proposed as an explanation of why more facially masculine males tend to take more risks (Apicella et al., 2008) and why they show increases in circulating testosterone after a success (Pound et al., 2009). Alternatively, as less masculine males are less attractive to females (Johnston, 2006), their behaviour tends to be more cooperative in order to signal their willingness to deliver high paternal investment and, therefore, their interest in long-term relationships (Takahashi et al., 2006).

The present paper aimed to integrate the different approaches used in Economics on the one side and Physiology on the other. Economic behaviour is based on the concept of preferences, which are revealed through individual choices. In Biology, some fundamental individual characteristics, like hormone levels (during development and in adults), have been described to have an impact on behaviour. Our two studies were designed to combine these two approaches and also to evaluate their relative importance. Clearly, the interplay between these two sets of explanations is a very complex issue that deserves further tests and analyses.

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References

Apicella, C.L., Dreber, A., Campbell, B., Gray, P.B., Hoffman, M. & Little, A.C. (2008). Testosterone and financial risk preferences. — Evol. Hum. Behav. 29: 384-390.

Archer, J. (2006). Testosterone and human aggression: An evaluation of the challenge hypothesis. — Neurosc. Biobehav. Rev. 30: 319-345.

Balliet, D., Parks, C., & Joireman, J. (2009). Social values orientation and cooperation in social dilemmas: A meta-analysis.— Group. Process. Interg. 12: 533-547.

Bates, T.C. (2007). Fluctuating asymmetry and intelligence. — Intelligence 35: 41-46.

Benderlioglu, Z., Sciulli, P.W. & Nelson, R.J. (2004). Fluctuating asymmetry predicts human reactive aggression. — Am. J. Hum. Biol. 16: 458-469.

Berenbaum, S.A. & Beltz, A.M. (2011). Sexual differentiation of human behaviour: Effects of prenatal and pubertal organizational hormones. — Front. Neuroendicronol. 32: 183-200

Binmore, K. & Shaked, A. (2010). Experimental Economics: Where next? — J. Econ. Behav. Organ. 3: 87-100.

Bolton, G.E. & Ockenfels, A. (2000). ERC: A theory of equity, reciprocity and competition. — Am. Econ. Rev. 90: 166-193.

Bribiescas, R.G. (2001). Reproductive ecology and life history of the human male. — Yrbk. Phys. Anthropol. 44: 148 –176.

Buchanan, C.M., Eccles, J.S. & Becker, J.B. (1992). Are adolescents the victims of raging hormones: evidence for activational effects of hormones on moods and behaviour at adolescence. — Psychol. Bull. 111: 62-107.

Burnham, T.C. (2007). High-testosterone men reject low ultimatum game offers. — Proc. R. Soc. B 274: 2327-2330.

Carré, J.M. & McCormick, C.M. (2008). In your face: facial metrics predict aggressive behaviour in the laboratory and in varsity and professional hockey players. — Proc. R. Soc. B 275: 2651–2656.

Cesarini, D., Dawes, C.T., Fowler, J.H., Johannesson, M., Lichtenstein, P. & Wallace, B. (2008). Heritability of cooperative behaviour in the trust game. — Proc. Natl. Acad. Sci. USA 105: 3721–3726.

Charness, G. & Rabin, M. (2002). Understanding social preferences with simple tests. — Q. J. Econ. 117: 817-869.

Charness, G. & Grosskopf, B. (2001). Relative payoffs and happiness: an experimental study. — J. Econ. Behav. Organ. 45: 301-328.

Crockett, M.J., Clark, L., Tabibnia, G., Lieberman, M.D. & Robbins, T.W. (2008). Serotonin modulates behavioural reactions to unfairness. — Science 320: 1739.

Eek, D. & Gärling, T. (2006). Prosocials prefer equal outcomes to maximizing joint outcomes. — Brit. J. Soc. Psychol. 45: 321-337.

Eisenegger, C., Naef, M., Snozzi, R., Heinrichs, M. & Fehr, E. (2010). Prejudice and truth about the effect of testosterone on human bargaining behaviour. — Nature 463:356-359.

Engelmann, D. & Strobel, M. (2004). Inequality aversion, efficiency, and maximin preferences in simple distribution experiments. — Am. Econ. Rev. 94: 857-869.

Enlow, D.H. (1996). Essential of facial growth. Philadelphia: WB. Saunders Company.

Fehr, E. & Schmidt, K.M. (1999). A theory of fairness, competition, and cooperation. — Q. J. Econ. 114: 817–868.

Fehr, E. & Rangel, A. (2011). Neuroeconomic foundations of economic choice—Recent advances. — J. Econ. Persp. 25: 3–30.

Fink, B., Grammer, K., Mitteroecker, P., Gunz, P., Schaefer, K. Bookstein, F.L. & Manning, J.T. (2005). Second to fourth digit ratio and face shape. — Proc. R. Soc. B 272: 1995–2001.

Fink, B., Neave, N. & Seydel, H. (2007). Male facial appearance signals physical strength to women. — Am. J. Hum. Biol. 19: 82–87.

Fischbacher, U. (2007). Z-tree, Zurich toolbox for readymade economic experiments. — Exp. Econ. 10: 171-178.

Folstad, I. & Karter, A.J. (1992). Parasites, bright males, and the immunocompetence handicap. — Am. Nat. 159: 603–622.

Frank, R.H. (1987). Choosing the right pond: human behaviour and the quest for status. New York: Oxford Univ Press.

Furlow, B., Gangestad, S.W.& Armijo-Prewitt, T. (1998). Developmental stability and human violence. — Proc. R. Soc. B 265: 1-6.

Gospic, K., Mohlin, E., Fransson, P., Petrovic, P., Johannesson, M. & Ingvar, M. (2011). Limbic justice—amygdala involvement in immediate rejection in the Ultimatum Game. — PLoS Biology e1001054.

Johnston, V.S. (2006). Mate choice decisions: the role of facial beauty. — TRENDS Cogn. Sci. 10: 9-13.

Josephs, R.A., Sellers, J.G., Newman, M.L. & Mehta, P.H. (2006). The mismatch effect: When testosterone and status are at odds. — J. Pers. Soc. Psychol. 90: 999-1013.

Kleinbaum, D.G. & Klein, M.G. (2002). Logistic regression: a self-learning text, 2nd Edition. New York, New York: Springer.

Klingenberg, C.P. & McIntyre, G.S. (1998). Geometric morphometrics of developmental instability: analyzing patterns of fluctuating asymmetry with Procrustes methods. — Evolution 52: 1363-1375.

Klingenberg, C.P., Barluenga, M. & Meyer, A. (2002). Shape analysis of symmetric structures: quantifying variation among individuals and asymmetry. — Evolution 56: 1909-1920.

Knafo, A., Israel, S., Darvasi, A., Bachner-Melman, R., Uzefovskyet, F., Cohen, L., Feldman, E., Lerer, E., Laiba, E., Raz, Y., Nemanov, L., Gritsenko, I., Dina, C., Agam, G., Dean, B., Bornstein, G. & Ebstein, R.P. (2008). Individual differences in allocation of funds in the dictator game associated with length of the arginine vasopressin 1a receptor RS3 promoter region and correlation between RS3 length and hippocampal mRNA. — Genes Brain Behav. 7: 266–275.

Kosfeld, M., Heinrichs, M., Zak, P.J., Fischbacher, U. & Fehr, E. (2005). Oxytocin increases trust in humans. — Nature 435: 673-676.

Little, A.C. & Jones, B.C. (2006). Attraction independent of detection suggests special mechanisms for symmetry preferences in human face perception. — Proc. R. Soc. B 273: 3093-3099.

Lutchmaya, S., Baron-Cohen, S., Raggatt, P., Knickmeyer, R. & Manning, J.T. (2004). 2nd to 4th digit ratios, fetal testosterone and estradiol. — Early Hum. Dev. 77: 23–28.

Manning, J.T. & Wood, D. (1998). Fluctuating asymmetry and aggression in boys. — Hum. Nat. 9: 53-65.

Mazur, A. & Booth, A. (1998). Testosterone and dominance in men. — Behav. Brain Sci. 21: 353-397.

Millet, K. (2011). An interactionist perspective on the relation between 2D:4D and behaviour: An overview of (moderated) relationships between 2D:4D and economic decision making. — Pers. Indiv. Differ. 51: 397-401.

Millet, K. & Dewitte, S. (2006). Second to fourth digit ratio and cooperative behaviour. — Biol. Psychol. 71: 111–115.

Millet, K. & Dewitte, S. (2009). The presence of aggression cues inverts the relation between digit ratio (2D:4D) and prosocial behaviour in a dictator game. — Br. J. Psychol. 100: 151–162.

Møller, A.P. (1997). Developmental stability and fitness: A review. — Am. Nat. 149: 916-942.

Møller, A.P. (2006). A review of developmental instability, parasitism and disease. Infection genetics and evolution. — Infect. Genet. Evol. 6: 133–140.

Morris, J.A., Jordan, C.L. & Breedlove, S.M. (2004). Sexual differentiation of the vertebrate nervous system. — Nat. Neurosci. 7: 1034-1039.

Muehlenbein, M.P. & Bribiescas, R.G. (2005). Testosterone-mediated immune functions and male life histories. — Am. J. Hum. Biol. 17: 527–558.

Murphy, R.O. & Ackermann, K. (2012). A review of social preferences measurement methods. In press.

Murphy, R.O., Ackermann, K. & Handgraaf, M. (2011). Measuring social value orientation. — Judgm. Decis. Mak. 6: 771–781.

Page, K.M., Nowak, M.A. & Sigmund, K. (2000). The spatial Ultimatum game. — Proc. R. Soc. B 267: 2177–82.

Palmer, A.R. & Strobeck, C. (1986). Fluctuating asymmetry: Measurement, analysis, patterns. — Ann. Rev. Ecol. Syst. 17: 391-421.

Pound, N., Penton-Voak, I.S. & Surridge, A.K. (2009). Testosterone responses to competition in men are related to facial masculinity. — Proc R Soc B 276: 153–159.

Rhodes, G. (2006). The evolutionary psychology of facial beauty. — Annu. Rev. Psychol. 57: 199- 226.

Rhodes, G., Chan, J., Zebrowitz, L.A. & Simmons, L.W. (2003). Does sexual dimorphism in human faces signal health? — Proc. R. Soc. B 270: S93–S95.

Roberti, J.W. (2004). A review of behavioural and biological correlates of sensation seeking. — J. Res. Pers. 38: 256-279.

Roth, A.E. (1995). Bargaining experiments. In: JH. Kagel and AE. Roth (Eds) The Handbook of Experimental Economics (pp. 253-348). Princeton: Princeton Univ Press.

Rupp, H.A. & Wallen, K. (2007). Relationship between testosterone and interest in sexual stimuli: The effect of experience. — Horm. Behav. 52: 581–589.

Salvador, A. (2005). Coping with competitive situations in humans. — Neurosc. Biobehav. Rev. 29: 195–205.

Sanchez-Pages, S. & Turiegano, E. (2010). Testosterone facial symmetry and cooperation in the prisoners' dilemma. — Physiol. Behav. 99: 355–361.

Scheib, J.E., Gangestad, S.W. & Thornhill, R. (1999). Facial attractiveness symmetry and cues to good genes. — Proc. R. Soc. B 266: 1913-1917.

Schaefer, K., Lauc, T., Mitteroecker, P., Gunz, P. & Bookstein, F.L. (2006). Dental arch asymmetry in an isolated Adriatic community. — Am. J. Phys. Anthropol. 129: 132–42.

Sisk, C.L., Schulz, K.M. & Zehr, J.L. (2003). Puberty: A finishing school for male social behaviour. — Ann. NY Acad. Sci. 1007: 189–198.

Sisk, C.L. & Zehr, J.L. (2005). Pubertal hormones organize the adolescent brain and behaviour. — Front. Neuroendocrin. 26: 163–174.

Smith, V.L. (1987). Experimental methods in Economics. In: The New Palgrave: A Dictionary of Economics. Vol 2. London: Macmillan.

Takahashi, C., Yamagishi, T., Tanida, S., Kiyonari, T. & Kanazawa, S. (2006). Attractiveness and cooperation in social exchange. — Evol. Psych. 4: 315-329.

Trivers, R. (2004). Mutual benefit at all levels of life. — Science 304: 964-965.

Van den Bergh, B. & Dewitte, S. (2006). Digit ratio (2D:4D) moderates the impact of sexual cues on men's decisions in ultimatum games. — Proc. R. Soc. B 273: 2091-2095.

Van Dongen, S. & Gangestad, S.W. (2011). Human fluctuating asymmetry in relation to health and quality: a meta-analysis. — Evol. Hum. Behav. 32: 380-398.

Van Lange, P., Otten, W., De Bruin, E. & Joireman, J. A. (1997). Development of prosocial, individualistic and competitive orientations: Theory and preliminary evidence. — J. Pers. Soc. Psychol. 74: 733-746.

Wallace, B., Cesarini, D., Lichtenstein, P. & Johannesson, M. (2007). Heritability of ultimatum game responder behaviour. — Proc. Natl. Acad. Sci. USA 104: 15631–15634.

Wilson, R.K. & Eckel, C.C. (2006). Judging a book by its cover: Beauty and expectations in the trust game. — Polit. Res. Q. 59: 189-202.

Yamagishia, T., Horita, Y., Mifune, N., Hashimoto, H., Lie, Y., Shinada, M., Miura, A., Inukai, K., Takagishi, N., and Simunovic, D. (2012). Rejection of unfair offers in the ultimatum game is no evidence of strong reciprocity. — Proc. Natl. Acad. Sci. USA 109: 20364–20368.

Zaatari, D. & Trivers, R. (2007). Fluctuating asymmetry and behaviour in the ultimatum game in Jamaica. — Evol. Hum. Behav. :28: 223– 227.

Zaatari, D., Palestis, B.G. & Trivers, R. (2009). Fluctuating Asymmetry of responders affects offers in the Ultimatum Game oppositely according to attractiveness or need as perceived by proposers. — Ethology 115: 627–632.

Zak, P.J., Kurzban, R., Ahmadi, S., Swerdloff, R.S., Park. J., Efremidze, L., Redwine, K., Morgan, K. & Matzner, W. (2009). Testosterone administration decreases generosity in the Ultimatum Game. — PLoS ONE 4: e8330.

Zak, P.J., Stanton, A.A. & Ahmadi, S. (2007). Oxytocin increases generosity in humans. — PLoS ONE 2: e1128.

Zethraeus, N., Kocoska-Maras, L., Ellingsen, T., von Schoultz, B., Hirschberg, A.L. & Johannesson, M. (2009). A randomized trial of the effect of estrogen and testosterone on economic behaviour. — Proc. Natl. Acad. Sci. USA 106: 6535-6538.

Zheng, Z. & Cohn, M.J. (2011). Developmental basis of sexually dimorphic digit ratios. — Proc. Natl. Acad. Sci. USA 108:16289–16294.

Zitzmann, M. & Nieschlag, E. (2001). Testosterone levels in healthy men and the relation to behavioural and physical characteristics. — Eur. J. Endocrinol. 144: 183-197.

Figure Legends

Figure 1

Differences across behavioural types

A) Differences in the individual features studied.

B) Differences in the rejection rates for the low and medium offers

C) Differences in the offers made.

FA was transformed into Ln(100xFA). Different statistical test were applied depending on the characteristics of the variables studied (t test, χ^2 test and Kruskal-Wallis H test respectively). * for $p<0.05$, ** for $p<0.01$.

Table 1: Summary statistics.

	Average	SD	Max	Min
Facial masculinity	0.089	0.022	0.154	0.042
Fluctuating Asymmetry	0.035	0.014	0.084	0.016
2D:4D finger ratio	0.962	0.030	1.049	0.897
N	152	152	152	152

Table 2:

Average individual features according to participants' response to the two offers.

		n	Fluctuating Asymmetry Ln(100 x FA)	Facial masculinity	2D:4D finger ratio
Low offer	Reject	89	0.036±0.014	0.093±0.022	0.960±0.030
	Accept	63	0.034±0.014	0.084±0.022	0.964±0.030
			t_{150}=1.183 p=0.239	t_{150}=2.453 p=**0.015**	t_{150}=-0.792 p=0.430
Medium offer	Reject	48	0.036±0.015	0.092±0.022	0.958±0.029
	Accept	104	0.035±0.014	0.088±0.022	0.964±0.031
			t_{150}=0.232 p=0.817	t_{150}=0.895 p=0.372	t_{150}=-1.155 p=0.250

Table 3:

Logistic models for the rejection rates in the low and medium offers.

Offer	**MODEL**				**VARIABLE**				
	-2LL	Likelihood Ratio Test	df	p	variables	coef	Wald	df	P
Low	189.589	16.659	6	0.011	Constant	-3.039	0.283	1	0.595
					2D:4D	5.310	0.817	1	0.366
					Masculinity	-17.409	4.425	1	**0.035**
					FA	-0.380	0.588	1	0.443
					SP		8.256	3	**0.041**
					ES	-0.548	1.481	1	0.224
					C	-1.277	7.270	1	**0.007**
					IA	-1.077	1.560	1	0.212
Medium	177.137	12.454	6	0.053	Constant	-5.169	0.718	1	0.397
					2D:4D	6.966	1.238	1	0.266
					Masculinity	-5.248	0.410	1	0.522
					FA	0.081	0.026	1	0.872
					SP		10.064	3	**0.018**
					ES	0.030	0.003	1	0.953
					C	-1.084	6.183	1	**0.013**
					IA	-1.647	4.355	1	**0.037**

Logistic regressions for the low and medium offers. The models reported include the variables 2D:4D, fluctuating asymmetry (FA), facial masculinity (Masculinity) and social preferences (SP). The latter variable has four possible categories: Efficiency Seeker (ES), Competitive (C), Inequality Averse (IA) and Self Interested (the reference group). A series of models were run by including one additional variable at a time. We report only the last of these models.